A New Species of *Geodiscelis* (Hymenoptera: Colletidae: Xeromelissinae) from the Atacama Desert of Chile

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Abstract.—Geodiscelis longiceps Packer, new species, is described from northern Chile. Morphologically, it is somewhat intermediate between *Chilimelissa* and *Geodiscelis*, but is clearly more closely related to the latter as indicated by numerous synapomorphies such as the broad basal bands of appressed tomentum, long and thin hind tibial spurs, well developed mesotarsal setae in the female, large and well sclerotised proctiger, angulate mesal margin and elongate inner membranous process to the gonocoxites and absence of a ventroapical process to the gonobase. It differs from the type species of the genus in the enormously elongate head and mouthparts but otherwise normal glossa. Based upon character states shared by the new species and the type species of the genus, a revised diagnosis for *Geodiscelis* is provided. Some comments on the adaptive significance of extremely elongate heads in the Xeromelissinae are made.

The purpose of this paper is to bring attention to an unusual new species of xeromelissine, Geodiscelis longiceps Packer, recently collected in Tarapaca Province in the Atacama desert of Chile. It exhibits some characters intermediate between those of the type species of the genus, Geodiscelis megacephala Michener and Rozen, and species of the related genus Chilinnelissa and also a remarkable convergence in head shape to C. rozeni Toro and Moldenke. Nonetheless, it is clearly more closely related to G. megacephala than to any species of Chilimelissa and its array of morphological characteristics permits a more detailed definition of the genus Geodiscelis.

In the descriptions, diagnostic characteristics of the new species among all Xeromelissinae are italicized. Except for body length, wing length, head width and length measurements, relative sizes of various structures are given in graticule units solely to indicate relative dimensions rather than the absolute size of particular features. Relative puncture density is given in terms of the ratio of interspaces (i) to puncture diameters (d) and the following standard abbreviations are used: F, T, S for flagellomeres, and metasomal terga and sterna respectively, IOD for interocellar distance, OOD for ocellocular distance, UOD and LOD for upper and lower ocular distances respectively.

The photographs used in figure 1 were taken with a Nikon coolpix 990 digital camera and amalgamated into one figure using Adobe Photoshop 6.0. The SEM photograph for figure 2 was taken using a Hitachi S520 scanning electron microscope at 20KV.

Geodiscelis longiceps Packer, new species Figs 1–6

Diaguosis.—The new species is readily separated from all other species of Xeromelissinae through the combination of pale bands on the metasoma, malar space enormous (longer than compound eye), and maxillary palps of normal form without differentiation of the segments into enlarged basal and reduced apical ones (Fig. 1). Among the Xeromelissinae only some species of *Chilicola* subgenus *Pseudiscelis* have the combination of considerably enlarged malar space and unmodified max-

illary palps (albeit with seven, rather than six, segments) but these lack pale markings on the metasoma. Similarly, males of Xenochilicola diminuta Toro and Moldenke are the only previously known xeromelissines with yellow markings on the metasoma and unmodified palps, but their malar space is comparatively short: one quarter as long as the compound eye. Chilimelissa rozeni Toro and Moldenke shares the yellow markings and very elongate malar space but it has extreme modifications of the maxillary palps (Fig. 1). The new species shares with G. megacephala the presence of long hairs on the middle tarsus (although these are even more strongly developed, into a distinct rake, in the new species, Fig. 2), very long hind tibial spurs, the basal bands of apressed, scalelike pubescence on the metasomal terga (Fig. 1) and details of the male genitalia (Figs 3-5). It differs in certain key characteristics from the type and only other species of Geodiscelis in lacking elongate apical lobes to the glossa, in the absence of clavate hairs on the female foretarsus, in having toothed claws in both sexes and in having a narrow stigma. The enormous malar space in the new species makes it possible to tell the two congeneric species apart at a glance.

Description.—Male. Body length 4.3mm, wing length 2.3mm, head width 1mm.

Colouration: Black (metasoma dark brown) with following parts yellow: labrum; mandible; malar space; apical mark on clypeus; scape, anterior surface of pedicel and flagellum; mark on tegula; entire foreleg except for brown on base of coxa, dorsal marks on trochanter and femur and ventral mark on tibia; entire midleg except for dark brown coxa and dorsal surface of trochanter and basal half of femur (narrowly yellow ventrally) and ventral mark on tibia; ventral surfaces of hind coxa and trochanter, apical one third of femur, tibia except for posterior brown mark and hind basitarsus; apical bands and ventrally reflexed portions of all metasomal terga; all metasomal sterna except for brown S1 and basal brown triangle on S2.

Pubescence: White, thickened, almost scale-like, dense on lower paraocular area, margins of scutum, dorsolateral portion of propodeum and basal bands to T1–T4 (covering basal two-thirds of T1); apex of each of mesotarsomeres 1–4 with one extremely long seta, that on basitarsus longer than basitarsus (18:15), that of second mesotarsal segment as long as basitarsus.

Surface Sculpture: Integument somewhat shiny despite dense, though shallow, microsculpture; punctation shallow and sparse on clypeus and supraclypeal area, apparently absent on frons, vertex and paraocular area; very shallow, effaced, largely transverse but more dense (i \sim d) on scutum, difficult to discern on mesoscutellum and sides of thorax; dorsal surface of propodeum weakly rugulose basally, wrinkled apically.

Structure: HEAD: Considerably longer than mesosoma (61:46) and more than twice as long as broad (61:28); mouthparts very long and narrow, galeal blade twice as long as greatest breadth, prementum 15 times longer than greatest breadth; maxillary palps 6-segmented, all segments similar in structure, second segment the shortest, sixth segment the longest, total length less than $\frac{1}{5}$ as long as prementum; labial palps 4-segmented; labrum broader than long (17:11), apex rounded; mandible without preapical tooth; malar space enormous, longer than greatest dimension of compound eye (48:36), malar line absent; clypeus three times longer than greatest breadth which is just basal to epistomal lobes; supraclypeal area three times longer than wide; lower ocular tangent passing through basal one-fifth of supraclypeal area; compound eye broad, length to breadth 35:25, ventral margin flat and interrupting profile of gena in lateral view; upper ocular tangent passing below median ocellus; ocelloccipital distance greater than diameter of lateral ocellus (7:5); OOD:IOD 11:15; gena ⁵/₆ as long as greatest

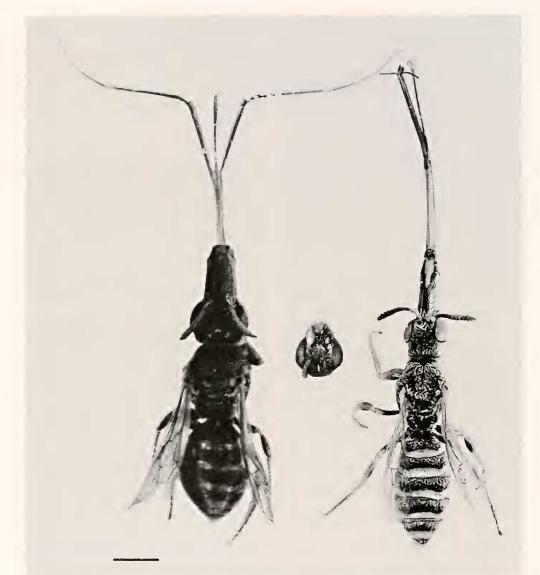


Fig. 1. Habitus photographs of *Geodiscelis longiceps*, right, and *Chilimelissa rozeni*, left, to show similarity in head shape and dissimilarity in mouthparts. Whereas the cardines and stipites of both species are elongate, the maxillary palps (artificially oriented laterad in both preparations) are enormous only in the latter species, the basal two segments being short, segments 3 and 4 being enormous, and the apical two segments again being short. Note that the maxillary palps of *C. rozeni*, when in use, extend considerably beyond the apex of the glossa whereas in *G. longiceps* the glossa attains the apex of the mouthparts. The head of *G. megacephala* is shown between the other two bees for comparison. Note that the pale metasomal bands of *C. rozeni* were artificially darkened in this specimen due to storage in buffered formalin. Scale line = 1mm.

width of compound eye; vertex in dorsal view slightly constricted behind compound eye; scape short, length to breadth 15:6; pedicel as broad as long, not narrowed towards base; F1 subtriangular, strongly narrowed towards base, remaining flagellomeres somewhat longer than broad, cylindrical.

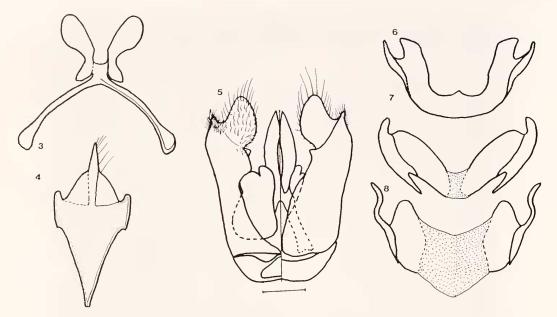
MESOSOMA: Elongate, distance from posterior margin of pronotal lobe to inser-



Fig. 2. Mesotarsal rake of female G. longiceps, SEM. Scale line = 0.1mm.

tion of metasoma greater than greatest depth of mesothorax (52:42); dorsal surface of propodeum depressed at base, concave in profile with slight swellings posterolaterally, longer than both metanotum and mesoscutellum (ratio of mesoscutellum:metanotum:dorsal surface of propodeum 11:7:13); legs unmodified other than for long setae on mesotarsus and hind tibial spurs very long and fine, longer spur more than two-thirds as long as basitarsus (23:36); stigma with margins basal to vein R diverging, portion in marginal cell slightly concave; first recurrent vein meeting first submarginal cross-vein, second recurrent vein on second submarginal cell.

METASOMA: Flattened, broadest at T3, pygidial plate absent; terminalia as in Figs



Figs 3–8. 3, *G. longiceps*, male, S7; 4, *G. longiceps*, male, S8; 5, *G. longiceps*, male, genital capsule; 6, *G. longiceps*, male, proctiger; 7, *G. megacephala*, male, proctiger; 8, *Chilimelissa australis*, male, proctiger. Ventral views on left, dorsal views on right. Scale line = 0. 1mm.

3–6; proctiger very large and well sclerotised appearing almost like a normal tergnm; S7 with somewhat elongate but comparatively well sclerotised apical lobes, basal lobes considerably reduced, almost absent; S8 elongate and narrow, apex narrowly rounded; gonobase lacking apicoventral projection; gonocoxites with strong apicomedian angle, gonostylus narrow, subapical median lobe large, surpassing posterior extremity of gonostylus.

Female: As in male except for usual secondary sexual characteristics and as follows: larger, body length 4.8mm, wing length 2.8mm, head width 1.1mm.

Colouration: With yellow mark on pronotal lobe, forefemur with larger dark mark.

Pubescence: More extensive on scutum and sides of mesothorax; basal hair bands of metasomal terga broader and present on T1–T5; foretarsus without clavate hairs; mesotarsus with well developed rake of long setae, considerably longer than basitarsus (up to 28:17, Fig. 2), mesobasitarsus with dense patch of shorter hairs along anterior margin; weak scopa on hind tibia; scopa of S2 composed of unbranched hairs.

Structure: Mandible with small preapical tooth; pedicel somewhat narrowed basally; F2–F9 shorter than broad; hind tibial spurs two-thirds as long as metabasitarsus; first and second recurrent veins originating on second submarginal cell; propodeum twice as long as metanotum, slightly shorter than mesoscutellum (ratio of lengths of mesoscutellum:metanotum: dorsal surface of propodeum 16:7:14).

Type material.—Holotype male, allotype female, 7 male and 19 female paratypes: CHILE, *Region 1, Tarapaca,* 29km marker on Hwy 687, 62km ESE of Pozo Almonte, S20°17'425" W069°12'97", 2510m 8–20.iv.2004, L. Packer, pan traps. An additional female, same data, is in glycerin and 8 females same data except 9.iv.2004, collected from flowers, are stored in alcohol. All specimens including the holotype and allotype are housed in the author's collection at York University with the exception of 2 individuals stored in alcohol which

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are in the Department of Entomology, Cornell University, Ithaca, New York. One female will be deposited in each of the following institutions: American Museum of Natural History, New York; the Snow Entomological Museum, University of Kansas, Lawrence, Kansas; USDA bee lab, Logan, Utah; Museo Bernardino Rivadavia, Buenos Aires, Argentina; Museo Nacional de Historia Natural, Santiago, Chile; and the Zoological Institute of St. Petersburg, Russia.

Etymology.—The specific epithet refers to the extreme elongation of the head in this species.

DISCUSSION

Based upon phylogenetic analysis of a large data set for all genera, subgenera and species groups of xeromelissine bees (Packer, in preparation), the new species shares numerous synapomorphies with G. megacephala, the type, and hitherto only, species of the genus. The following character states thus form a revised diagnosis for the genus Geodiscelis and are unique to it among all Xeromelissinae: elongate "rake" of hairs on the mesotarsus; basal bands of apressed scale-like tomentum to metasomal terga; hind tibial spur elongate, two-thirds as long as basitarsus, and fine, barely any more robust than some of the more elongate hairs on the hind tibia; proctiger well sclerotised with the two lateral portions almost (megacephala) or completely (longiceps) united; no apicoventral projection(s) to the gonobase; an apicomedial angulation on the gonocoxites; and membranous lobe of gonocoxites extending beyond the gonostylus.

These last two characters require comment. In their Fig. 5, Michener and Rozen (1999) show the apicoventral margin of the gonobase to be incomplete in *G. megacephala*, a condition that renders presence of an apicomedian angulation impossible as, when present, it would arise from a medial portion of the ventral surface of the gonobase. However, in the paratype

specimens of this species available to me, the apicoventral margin of the gonobase is complete as is the case in all Xeromelissinae, although in almost all other taxa it is elaborated into a narrow median projection (Xenochilicola, Chilimelissa, Xeromelissa) or it forms a broadly based apically concave lobe (Chilicola). The nature of the apical region of the gonocoxites also requires reinterpretation of the observations of Michener and Rozen (1999). These authors noted the double nature of the apical attachments to the gonocoxites, but considered the shorter one to represent an evolutionary novelty and the longer, more mesal one, to represent the gonostylus. This longer structure arises from the apicomedian surface of the gonocoxites rather than at the apex, and thus appears homologous to the smaller lobe found in most Chilimelissa species and also in Xeromelissa wilmattae Cockerell (see for example the illustration for Chilimelissa mucar, Fig. 327 in Toro and Moldenke, 1979). The condition described here for G. longiceps is intermediate between that of Chilimelissa and G. megacephala.

Additional features which serve to support the monophyly of Geodiscelis include the form of S7 and the distinct junction between gonocoxite and gonostylus. In G. megacephala the lobes of S7 are considerably reduced and entirely fused to the reduced disc. Geodiscelis longiceps represents an intermediate condition between Chilimelissa and G. megacephala in this feature as its lobes are also comparatively well sclerotised and simple, but are somewhat larger and slightly more complex in shape. Similarly, in both species the gonostylus is very well differentiated from the gonocoxites whereas in most Xeromelissinae the junction between these two structures tends to be poorly demarcated.

With *G. longiceps* showing some intermediate characteristics between *G. megacephala* and *Chilimelissa* species, it could be thought that *Geodiscelis* should be subsumed within the latter genus. However, phylogenetic analyses (Packer in preparation) indicate a sister group relationship between the two genera and the differences between the two do seem substantial, especially in mouthpart characters that are so often of importance in bee systematics.

All individuals of the species were collected in a small area where only two species of flowering plant were found. One is believed to be a member of the genus Maleslierbia (Malesherbiaceae) the other, upon which most bees seemed interested, is Tiquilia atacamensis (Phil.) A. Richardson (Boraginaceae). Interestingly, the type species of *Geodiscelis* forages exclusively on a species of *Heliotropium*, a closely related genus to *Tiquilia*, although the host of *G*. megacephala has smaller flowers than does T. atacamensis. The apparent host of G. longiceps has bright blue flowers and golden yellow anthers and although superficially it has an apparently open bowl-shaped structure, it has very deep nectaries (Gengler-Nowak, personal communication). Although most specimens were collected in pan traps adjacent to these plants, large numbers were observed on or flying over these two species of flowers, particularly the *Tiquilia*, or resting on sand adjacent to the plants. Search on additional Tiquilia patches at distances of 1, 3 and 10km to the East (all at higher altitude) failed to find additional specimens of G. lougiceps. The patches where *G. longiceps* was found represented the last vestiges of vegetation heading west from the more vegetated mid altitude Altos de Pica to the east and the vegetation-free desert of the eastern slopes of the Pampa del Tamarugal to the west. The locality is on the border between the arid Andean Piedmont and the interior "absolute" desert, an area with very small amounts of summer rain and rarely any winter rain (Caviedes 1973), but one which has experienced several periods of increased inundation since the last ice age (Betancourt et al. 2000).

The mesotarsal rake of females of the new species appears unique among the bees (they are not as well developed in G. *megacephala*), although similar structures are common among the sand wasps, albeit on the foretarsi (Bohart and Menke 1976). This feature strongly suggests that this species nests in sand, as is also known for the type species of its genus. Other than G. megacephala, the Xeromelissinae have been thought to be stem and twig nesting bees (Michener 2000, 2002). However, it has recently been demonstrated that at least one species of *Chilimelissa*, *C. australis* Toro and Moldenke, also nests in the sand (Packer 2004). Several hours of sifting of the loose sand that collects around the bases of the aforementioned plants and dissection of their dried stems failed to locate any brood cells of the new species.

The extreme elongation of the head and mouthparts of the new species are very reminiscent of C. rozeni. However, in the latter species the maxillary palps are considerably modified with segments 3 and 4 both being almost as long as the considerably elongated head such that when combined with the cardines and stipites, the mouthparts are longer than the total length of the body (Fig. 1). In G. longiceps the cardines and stipites are proportionately even longer than those of C. rozeni but the maxillary palps are entirely unmodified, totaling less than 1/4 the length of either the cardines or stipites and only one half as long as the malar space. One wonders about the adaptive significance of such elongate heads and mouthparts in these bees. Chilimelissa rozeni has been found foraging upon the flowers of Nolana alba Phil. to the east of Chañaral on either side of the border between Chile's regions II and III (Packer, Zayed and Grixti unpublished observations). This flower has a very long corolla and a very long tongue is required to reach the nectaries (as shown for Nolanomelissa toroi Rozen foraging on a related Nolana species by Rozen [2003]). It seems likely that the elongate maxillary palpi of C. rozeni causes nectar to move up to the glossa, which ends at

the base of the maxillary palpi, through capillary action. The enormous tongues of C. rozeni are clearly sometimes a liability in that it often takes the bees several seconds to retract them when disturbed whilst in the flowers and tongue retraction seems to be required before flight occurs (Packer, Zayed and Grixti, unpublished observations). Observations of foraging G. longiceps suggest a somewhat different explanation for the unusual head and mouthpart modifications in this species. While foraging for nectar, these bees do not enter the flowers, but instead, sit on the petals with their elongate heads in an approximately horizontal orientation over the open corolla of the flower. The long tongue then protrudes almost perpendicularly, ventral to the insect. It seems that the elongate tongue permits access to the deep nectaries while the insect remains on the top of the flower. This permits visual inspection of the surroundings while feeding, which is not possible when bees have their heads deep within the corollas of deeper flowers. Perhaps avoidance of predators is an adaptive explanation for this unusual combination of behaviour and morphology.

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